The ultrastructure, development, and systematic position of the graptolite genus *Mastigograptus*

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Bates, D.E.B. and Urbanek, A. 2002. The ultrastructure, development, and systematic position of the graptolite genus *Mastigograptus*. *Acta Palaeontologica Polonica* 47 (3): 445–458.

Fragments of rhabdosomes isolated by chemical treatment from an erratic boulder of Baltic origin and ?Middle Ordovician age, provisionally assigned to *Mastigograptus* aff. *tenuiramosus* (Wallcott, 1881) were studied with SEM. Although exceptionally well preserved, remains lack the thin-walled free portions of thecae. Rhabdosomes are provided with a strongly developed basal disc, short stem and many branched stipes. The latter consist of heavily corticalized chains of stolothecae with alternately disposed thecal bases. Stolothecae display a morphological gradient and increase in size and change in shape distalwards. The stolon system studied with SEM on naturally and artificially broken specimens, as well as traced through open thecal bases, reveals a regular triad budding but no stolon inside the stolothecal cavity. We tentatively suggest that crassal lining, recognized earlier by TEM studies, corresponds to an unusually inflated stolonal stolon, filling the entire thecal cavity and adhering tightly to stolothecal wall. The systematic position of *Mastigograptus*, a matter of long debate, seems to be defined by a number of structural features which imply a distinct difference between genus in question and all known orders of sessile graptolites. The order Mastigograptida nov. and the family Mastigograptidae nov. are proposed.

Key words: Pterobranchia, Graptolithina, *Mastigograptus*, Ordovician, ultrastructure, astogeny, taxonomy.

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Introduction

Mastigograptus Ruedemann, 1908 is a sessile graptolite with dendroid appearance, whose systematic position, in spite of numerous papers dealing with its morphology, remains uncertain. In the course of taxonomic debate it has been placed among hydroid coelenterates, assigned to dendroid or dithecoid graptolites, or most frequently treated as a graptolite genus whose order and family are uncertain (see Systematic position, below). The aim of the present paper is to study the general morphology of the rhabdosome, the stolon system and budding pattern, as well as the ultrastructure of the rhabdosome, on the basis of ample and exceptionally well preserved material, isolated from Baltic drift boulders of ?Middle Ordovician age, by chemical treatment. As far as the ultrastructure is concerned, the present SEM study is complementary to that of Urbanek and Towe (1974), who examined ultrathin sections with TEM and to Andres (1980) who using SEM recognized only main skeletal fabrics. The new evidence obtained is used i.a. to draw some taxonomic conclusions.

Previous studies on *Mastigograptus* from Baltic drift boulders

The graptolite genus *Mastigograptus* was erected by Ruedemann (1908) for the species *Dendrograptus tenuiramosus* Walcott, 1879, and described by him on the basis of flattened material. Eisenack (1934: figs. 20–22) was the first to describe isolated remains of *Mastigograptus*, recovered from Baltic erratic boulders by chemical treatment and identified by him as objects of unknown affinity. However, his fine illustrations leave no doubt that the object in question is congeneric and probably also conspecific with *Mastigograptus*, as described later by Andres (1961). Kozłowski (1959, 1962, 1965, 1966) etched *Mastigograptus* remains from several Baltic erratic boulders, and made a number of morphological and palaeobiological observations on them which he partly described or mentioned in his papers. He was probably the first to identify these remains from Baltic drift material as representing the genus *Mastigograptus* (see Urbanek 1959). Urbanek and Towe (1974) studied fragments of *Mastigograptus*, etched from a Baltic erratic boulder, with the TEM.

They demonstrated an excellent state of preservation of skeletal tissues, presented evidence of the collagenous nature of the skeletal fabric and studied in some detail the basal disc. Some structural features recognized by Urbanek and Towe may be better understood in the light of the present contribution.

In his consecutive papers Andres (1976, 1977, 1980) dealt with pterobranchs and primitive graptolites from erratic blocks representing the so-called "Ostseekalk", a fine-grained limestone of Late Ordovician age. His papers represent great progress in understanding *Mastigograptus*, known heretofore only from the flattened specimens described mainly by Ruedemann (1908, 1947), and partly misunderstood by him (he was convinced of the hydroid affinity of the genus in question, and interpreted points of attachments as true thecae while the thin-walled free parts of thecae were considered by him as "conical appendages"). Andres provided evidence that the stipes of *Mastigograptus* are made of heavily "carbonized" stolothecae and that the attenuated free portions of the remaining thecae, which are essentially grouped in triads emerging at characteristic points of attachment ("Ansatzstellen"), displaying an alternate arrangement. Although the degree of thecal dimorphism (differentiation into auto- and bithecae) could not be established safely on the material available to Andres, nevertheless he assumed that it was probably smaller than that in dendroids and crustoids. His observations concerning the internal structure of the stipe below the point of attachment of a triad need re-interpretation in the light of our studies, and the entirety of knowledge concerning the budding in sessile Graptolithina.

Material and methods

All the specimens of *Mastigograptus* illustrated in the present paper (except Fig. 1H) were etched from an erratic boulder approxmately 2 kg in weight, collected at Mochty, in the valley of the Vistula River some 60 km N of Warsaw, central Poland. The boulder is a "grey, fine-grained, dull limestone" (Kozłowski 1960: 108), numbered O.334 in the collection of boulders in the Institute of Palaeobiology, Polish Academy of Sciences in Warsaw.

The specimen illustrated in Fig. 1H was etched from a light grey, organogenic limestone from the same locality and numbered O.181. The organic fossils were etched with acetic acid, cleaned from mineral impurities, and stored in glycerine.

The primary material consisted of a great number of many branched rhabdosomes. During decalcification large fragments of stipes gradually emerged from dissolving matrix, resembling hair, but broke up into many short lengths of stipe. Selected specimens, before mounting on SEM stubs, were washed in distilled water (and/or graded ethanol series) and placed on an adhesive tape in the droplet of fluid by the pipette or with a fine brush. Specimens coated with gold-palladium were examined with a Philips XL scanning microscope in the Institute of Palaeobiology, Warsaw or with a Jeol 840 in the University of Wales, Aberystwyth.

The light micrographs of the basal disc (Fig. 1H) were taken from thin sections obtained by the second author when working with T.M. Towe in 1971 at the Department of Paleontology, Smithsonian Institution, Washington D.C. Prior to sectioning with an LKB ultramicrotome using a diamond knife, specimens were embedded in Durcupan epoxy resin (Urbanek and Towe 1974).

Illustrated specimens have been deposited in the Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland (ZPAL) and numbered G.30/1–18.

Identification of specimens studied

As all the material illustrated comes from a single boulder O.334, and since some fragments show an intermediate morphology, while other characters, such as the length of segments, are uniform, it is proposed that all the material comes from a single species. The slender stipes figured by Andres (1977: figs. 14–16) are so similar in morphology and dimensions that they probably come from the same species. He emphasized a specially close relationship between of the species he described by him from the "Ostseekalk" boulders and *Mastigograptus tenuiramosus* (Walcott, 1881) from the Utica Shale of North America. Whether the Baltic form is really conspecific with the North American one is at the moment difficult to establish safely, mainly because the American material is imperfectly known and needs revision. In view of the rather high degree of endemism exhibited by sessile graptolite faunas, conspecificity seems rather uncertain. Consequently, the most reasonable solution is to identify of the taxon described herein as *Mastigograptus* aff. *tenuiramosus* (Walcott, 1881). It appears to be very similar to *Mastigograptus tenuiramosus*, but may have the thecal bases more closely spaced; it also has amphora-like swellings in distal stolothecae, which Ruedemann (1908, 1947) noted in *Mastigograptus gracillimus* (Lesquereux, 1878).

Stratigraphic setting

Abundant and excellently preserved remains of *Mastigograptus* are associated in boulder O.334 with the following assemblage of acid-resistant fossils; Hydrozoa: *Rhabdohydra tridens* Kozłowski; Graptolithina: *Calyxdendrum graptoloides* Kozłowski, *Dictyonema* sp.; Chitinozoa: *Cyathochitina campanulaeformis* (Eisenack) and scolecodonts. Remains of *Calyxdendrum graptoloides* were found in other boulders in association with diplograptids indicating a Middle Ordovician age (Kozłowski 1960; Urbanek 1959). This may also be the age of boulder O.334. The age of boulder O.181, with equally abundant *Mastigograptus* (probably conspecific with *M.* aff. *tenuiramosus*) was discussed by

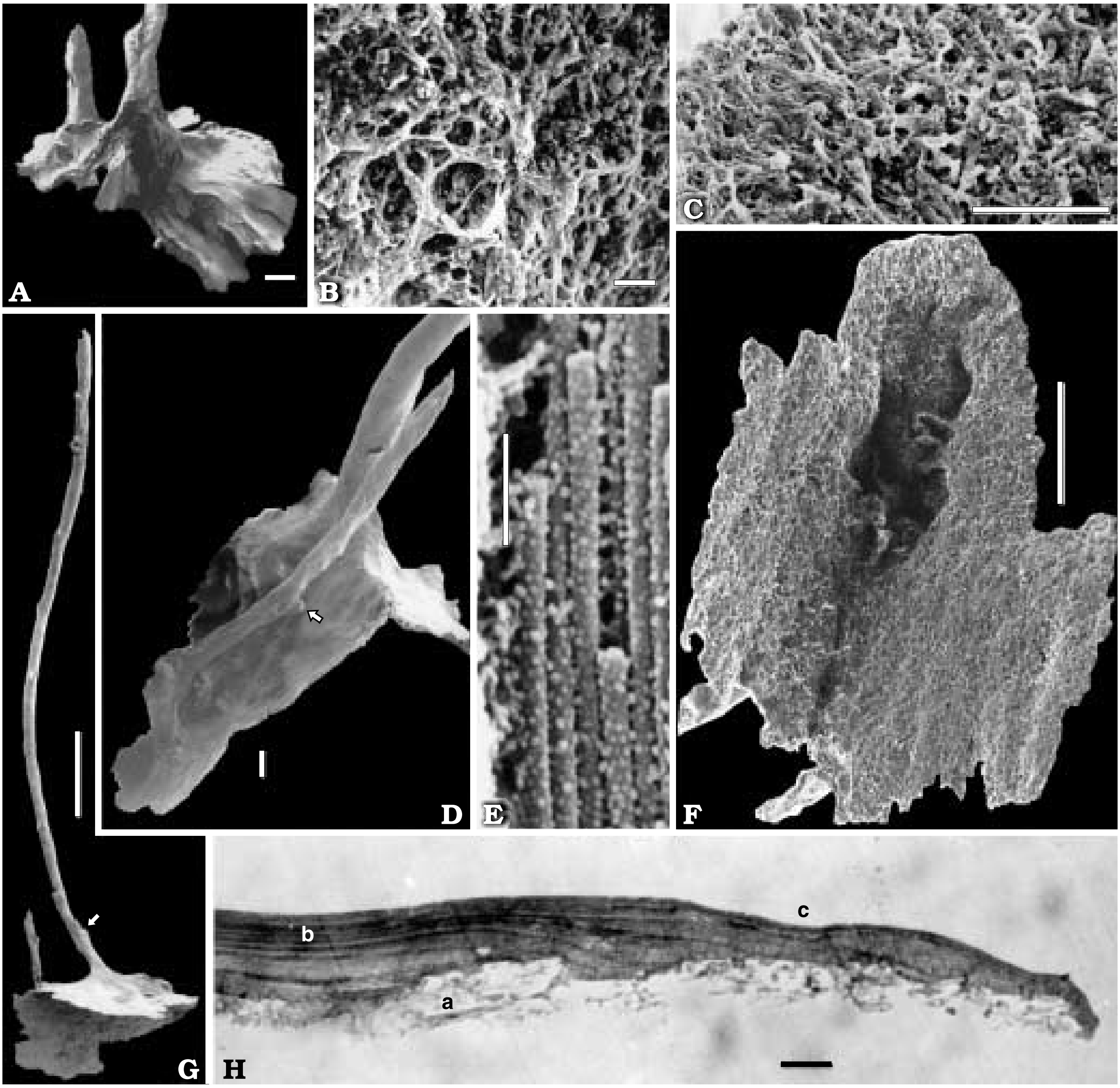

Fig. 1. *Mastigograptus* aff. *tenuiramosus*. **A**. Holdfast with two siculae (ZPAL G.30/1). Scale bar 100 µm. **B**. Spongy meshwork texture of the basal layer "a" of holdfast (ZPAL G.30/1). Scale bar 10 µm. **C**. Spongy meshwork of basal layer "a" with fibrils forming clumps or "trabeculae" (ZPAL G.30/2). Scale bar 100 µm. **D**, **F**, **G**. Holdfast and two stems: lateral view with inclined sicula; lower surface of holdfast with imprint of the ribs of a shell; lateral view. Arrows show position of sicular aperture (ZPAL G.30/2). Scale bars: **D**, 100 µm; **F**, 500 µm; **G**, 1 mm. **E**. Parallel fibrils in holdfast, with coating of small "blebs" of material (ZPAL G.30/2). Scale bar 500 µm. **H**. Light micrograph of section through holdfast. *a*, irregular basal layer; *b*, thin parallel laminae; *c*, thicker peripheral laminae. Scale bar 10 µm.

Urbanek (1959). None of the fossils found in the assemblage is diagnostic of a precise stratigraphic horizon. They display a wide stratigraphic range (Lower–Upper Ordovician). The presence in boulder O.181 of a diplograptid resembling the lasiograptid *Lasiograptus retusus* Lapworth may indicate a Llandeilo–Llanvirn age, but the specimen is too fragmentary to be sure. However, a Middle Ordovician (Viruan) age for both boulders O.181 and O.334 seems reasonable. Therefore specimens described herein are somewhat older than Andres' ones, which are probably Upper Ordovician (Harjuan).

General morphology

The material available includes all portions of the rhabdosome: three specimens with holdfasts and short lengths of unbranched stipe (Fig. 1A, G), as well as a number of pieces of stipes, some showing branching (Fig. 3D). The basal discs appear to be moulded to fit the underlying substrate. Proximal portions of stipes are made of slender parallel-sided stolothecae, with relatively thin walls; distal portions are amphora-shaped stolothecal segments, with thicker walls and more robust lateral thecal groupings. Some specimens are long enough to show a transition between the two types of stipe segment; they reveal a gradual astogenetic change in size and shape of the stolothecal segments, from proximally tubular to distally more inflated (amphorate) (Figs. 1G, 3D, G, 7E). This indicates that *Mastigograptus*, unlike the vast majority of described sessile representatives of Graptolithina, displays a morphological gradient operating along the stipes of the rhabdosome. Whether this tendency towards greater size at distal end includes also free thecae is at present unknown.

However, in spite of its otherwise excellent state of preservation, the material studied is incomplete: the thin-walled, free portions of the thecae are absent, and only the thecal bases have survived. In the light of observations made by Ruedemann (1908), the rhabdosomes which lack completely the thin-walled free portions of the thecae may be considered the characteristic state of preservation in *Mastigograptus*. He suggested that free portions of thecae (his "conical appendages"), as fragile and fused to the rhabdosome by the narrow base of attachement alone, "were very easily detached and lost" (Ruedemann 1908: 212). Isolated free portions of the thecae may be found loose on the slab.

Basal disc

Mastigograptus displays a strongly developed and frequently exceptionally well preserved basal disc, which makes it a model example of a discophorous graptolite, as defined by Kozłowski (1971). The basal disc has been illustrated by Eisenack (1934: figs. 20–22) and Andres (1961: fig. 2A; 1977: figs. 15, 16). Ruedemann (1947), in his amply illustrated description of Cambrian to Silurian *Mastigograptus*, does not mention basal discs. The only dendroid basal discs comparable in size and state of preservation to our specimens are those described by Kozłowski (1949: pl. 6: 5, 6; pl. 10: 1, 5) in *Dendrograptus communis*, *D. regularis* and *Rhipidodendrum samsonowiczi*, all isolated from Tremadocian cherts with HF. In our material the basal disc is roughly circular and up to about 2 μm in diameter (Fig. 1D, F, G). The upper surface is smooth and passes up into the cortex of the sicula and stem; the lower surface is rough and appears to be moulded to the form of the substrate to which it adheres. This is particularly well shown in a specimen (Fig. 1D, F, G), where the holdfast is sharply convex and moulded to a surface of low parallel ridges spaced at about 200? μm intervals, which itself must have been formed into a sharp keel, parallel to the faint ridges (Fig. 1F). This may have been part of a small shell, with the small ridges being either ribs or growth lamellae. Eisenack (1934, confirmed by Andres 1977), mentioned that one of his basal discs bore the imprint of the punctations of a brachiopod shell. In two of our three specimens there is an additional sicula which, in specimen shown on Fig. 1D, F, G has also grown into a stem (Fig. 2E) is broken at the level of the sicular aperture.

As shown in the thin sections illustrated by Urbanek and Towe (1974: pls. 23–25), the basal disc comprises successive laminae formed over an irregular basal layer (*a*, Fig. 1H). Succeeding laminae (*b*, Fig. 1H) overlap each other peripherally, thickening and becoming less dense (*c*, Fig. 1H) as they do so.

The fabric of basal layer *a* is formed of fibrils of variable diameter (1–10 μm), making an irregular spongy meshwork in which the fibrils appear to anastomose (Fig. 1B), leaving irregular spaces ("ocelli"), and also forming downward clumps (Fig. 1C). This fabric is also well seen in the TEM sections of Urbanek and Towe (1974: pl. 25). It is probable that the function of this fabric, which is not found anywhere else in the rhabdosome, was to penetrate the substrate.

The laminae *b* and *c* are formed of units of three fabrics (1–3) in different proportions:

(1) an irregular meshwork of randomly oriented fibrils, 100–200 nm in diameter (Fig. 2A); this fabric is comparable with that of graptoloid and dendroid fusellar tissue;

(2) parallel fibrils of the same diameter, forming successive sheets of fibrils with (Fig. 2C, D) or without (Fig. 2B) lamellae of sheet fabric between; the fibrils may be grouped together in bundles (Fig. 2D), recalling those seen in the cortex of some dendroids (Urbanek and Towe 1974: pl. 11);

(3) layers of granular sheet fabric with scattered vesicles (Fig. 2C, D), similar to those bounding both fuselli and cortical bandages in dendroids and graptoloids (Crowther 1981: pls. 10–13).

In overall make-up these three fabrics are grouped into cortical units which form the laminae seen in Urbanek and Towe's thin section and TEM sections. The parallel fibrils of successive units show varying directions, but we have not been able to determine whether they form parallel-sided bandages. Each unit can consist of all three fabrics, laid down in the order 1–3, or with the sheet fabric (3) omitted between successive units. The fusellar fabric (1) is lacking or only incipiently developed towards the centre of the holdfast, but it becomes thick towards the periphery. It appears then that a unit may be more fusellus-like towards the margin of the holdfast, where, as an increment of growth it is increasing the area of the holdfast, but more bandage-like towards the centre where it is adding to the thickness, and especially the strength, of the cortex. Around the margin of the holdfast, there is a tendency for the parallel fibrils to be orientated radially; radial fibrils should strengthen to the holdfast better than concentric ones.

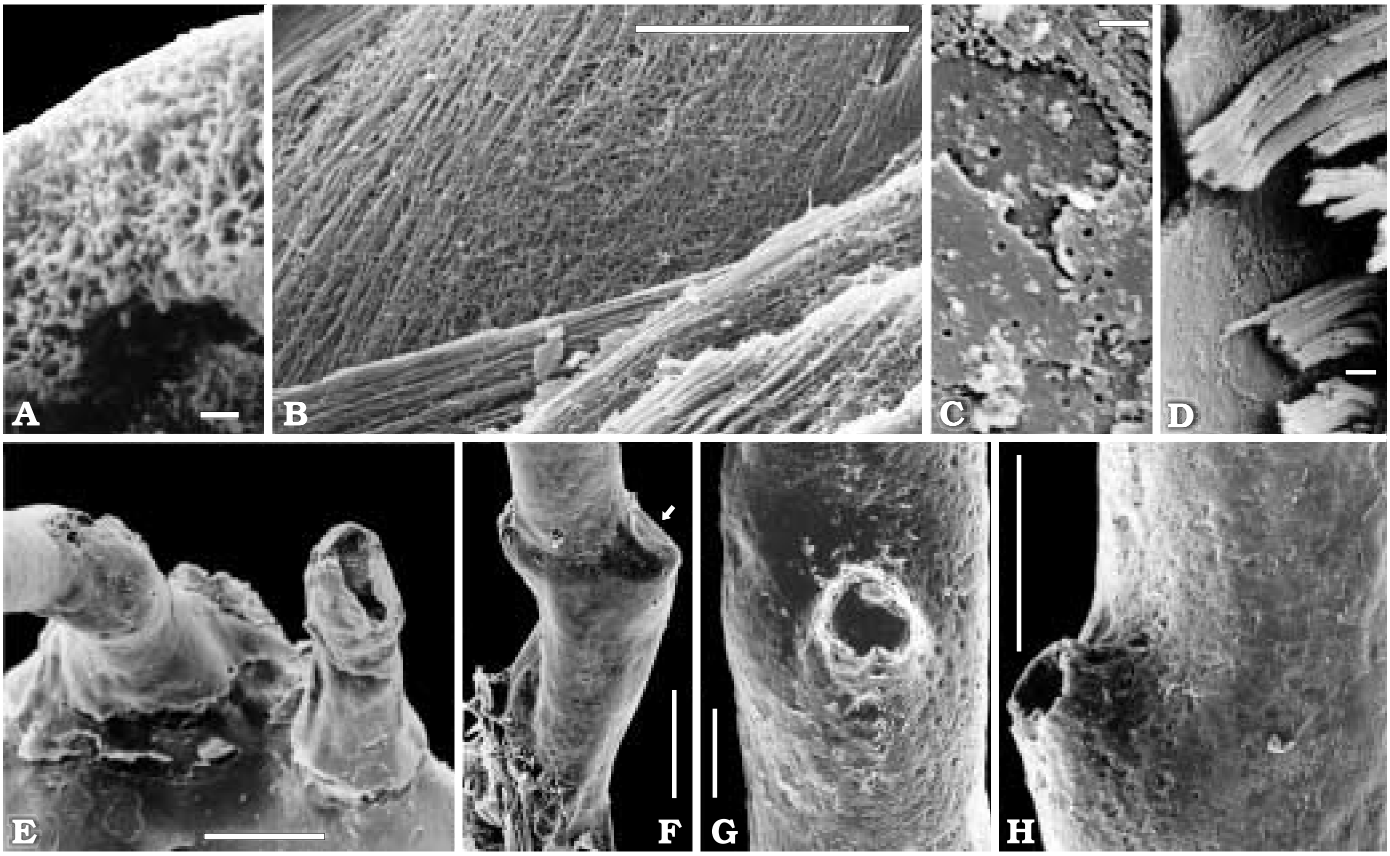

Fig. 2. *Mastigograptus* aff. *tenuiramosus*. **A**. Fusellar fabric of holdfast (ZPAL G.30/2). Scale bar 1 µm. **B**. Fusellar and cortical fabrics in the laminae of holdfast (ZPAL G.30/3). Scale bar 20 µm. C. Sheet fabric of laminae of holdfast (ZPAL G.30/1). Scale bar 1 µm. **D**. Laminae of holdfast. Bundled parallel cortical fibrils and sheet fabric with vesicles (ZPAL G.30/1). Scale bar 1 µm. **E**. Two siculae on holdfast. The left hand one is occluded (ZPAL G.30/1). Scale bar 100 µm. **F**. Occluded sicula (arrowed) (ZPAL G.30/3). Scale bar 100 µm. **G**, **H**. Broken thecal base on proximal portion of stem (ZPAL G.30/2). Scale bars: **G**, 50 µm; **H**, 100 µm.

Sicula

The initial segment of the stem or basal part of the stipe, which we presume to be the sicula, forms a cylinder over 100 µm in diameter and 300 µm high (Figs. 1A, D, G, 2E, F, 3C). However, the total length of the sicula is probably considerably more, since the base of the sicula should sit on the substrate, and the basal disc will have been thickened around it. At the top of this segment, the diameter of the stipe narrows abruptly to less than 100 µm, at an inwardly and upwardly inclined surface or ledge (Fig. 2F, arrow). This we interpret as the occluded aperture of the sicula.

Previous work on the astogeny of dendroids indicates that the next, and narrower, segment of the stipe should be the sicular stolotheca which will have issued from the side of sicula, and whose width should have contributed to the diameter of the sicula. However, this cannot be confirmed from the external form of the stipe, which in any case may have been so thickened by the addition of cortex to have smoothed out any such expression. Occlusion of the aperture of the sicula is doubtless secondary. It probably followed a degeneration of the siculozooid, which ceased to be active. Many instances of occlusion of auto- and bithecae (but not siculae) were described by Kozłowski (1949: 43–47, pl. 8: 7, 8) in dendroid and camaroid graptolites. He studied also the skeletal histology of occlusion, namely the formation of occlusion lamella, sealing the aperture (Kozłowski 1949: pl. 4: 9). According to his data, occlusion is especially frequent in the basal parts of colonies, as well as in terminal, growing parts of branches. A characteristic feature of occlusion is its local effect: while a given theca is occluded, neighbouring thecae show no traces of abnormality. This is also the case with occlusion recorded in the budding process of many triads in the more distal parts of stipes in our *Mastigograptus* (described below).

In specimen shown on Fig. 1G, it is of interest to note that the two siculae are attached to the basal disc at different places: one, which produced the major stem, on the keel, and the other on a flank. The stem formed by the latter makes an abrupt angle with the sicula, but is parallel to the major stem. Perhaps the two stipes grew vertically, but the sicula of the smaller stipe was forced to attach itself at roughly right angles to the substrate. In passing it should be noted that, if our "two siculae"

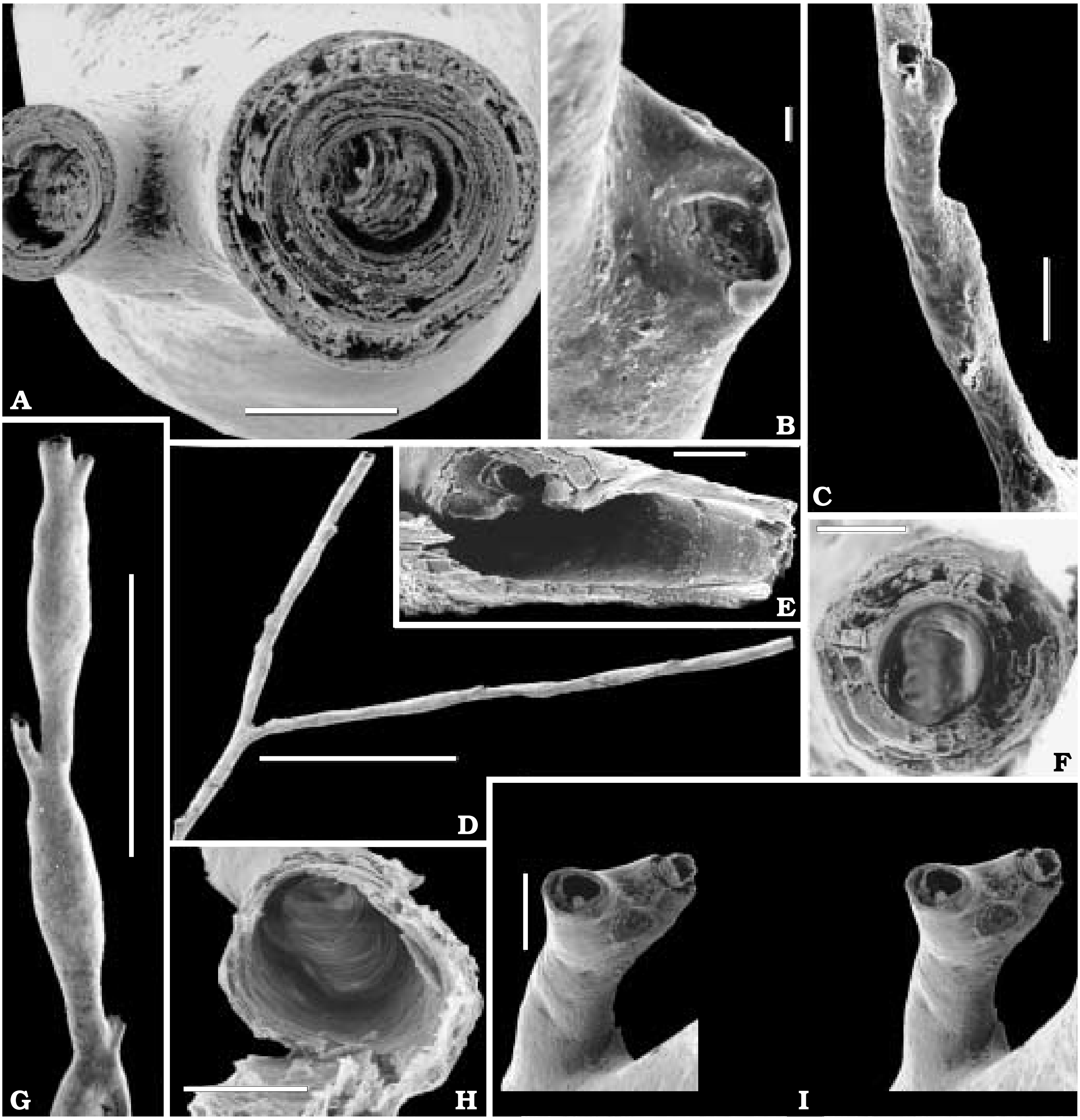

Fig. 3. *Mastigograptus* aff. *tenuiramosus*. **A**. Stipe with thick cortex and fractured thecal base. (ZPAL G.30/4). Scale bar 100 µm. **B**. Occluded thecal base on proximal portion of stem (ZPAL G.30/3). Scale bar 10 µm. **C**. Proximal portion of stem, with occluded sicula and first thecal base. (ZPAL G.30/2). Scale bar 200 µm. **D**. Portion of stem with monopodial branch (ZPAL G.30/5). Scale bar 2 µm. **E**. Fractured stolotheca; distal to left (ZPAL G.30/6). Scale bar 50 µm. **F**. Fractured stem with thick cortex and borings (ZPAL G.30/7). Scale bar 50 µm. **G**. Amphorate stolothecae, and broken thecal bases (ZPAL G.30/4) Scale bar 1 mm. **H**. Amphorate stolotheca, looking proximally. (ZPAL G.30/8). Scale bar 100 µm. **I**. Stereopair view of thecal base (ZPAL G.30/4). Scale bar 100 µm.

interpretation of this specimen is correct, the holdfast is therefore compound and has been secreted by both colonies. Hence one can assume that, during life, *Mastigograptus* colonies did not display any allelopathic interactions.

In general, the sicula of *Mastigograptus* resembles most the cylindrical (tubular) siculae of dendroid graptolites. It differs both from the “embryonic vesicle” of *Rhabdopleura* and from the conical sicula of *Dendrotubus*.

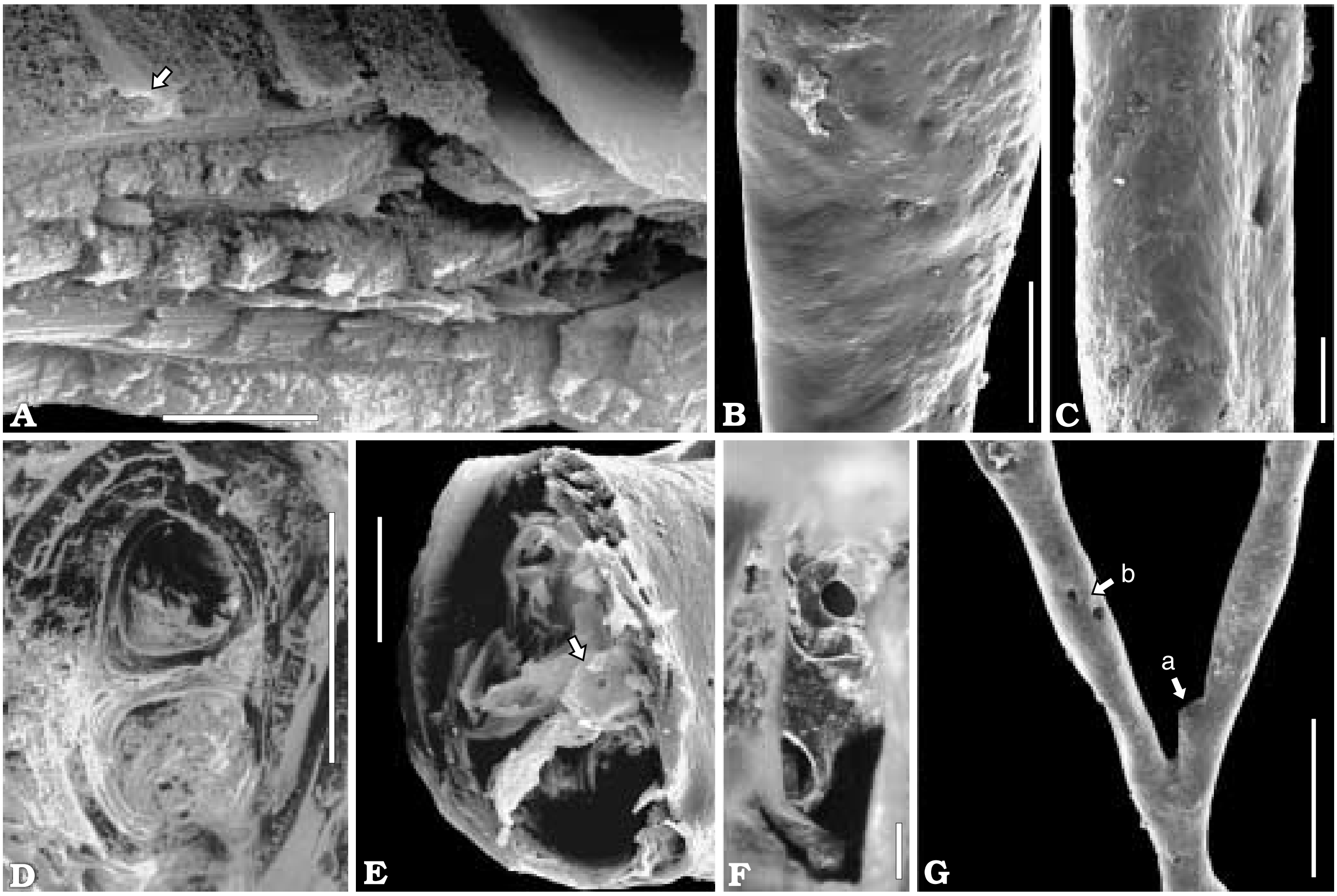

Fig. 4. *Mastigograptus* aff. *tenuiramosus*. **A**. Fractured wall of stolotheca. The head of a fusellus is arrowed (ZPAL G.30/9). Scale bar 10 µm **B**, **C**. External ornament on stolothecae (ZPAL G.30/10). Scale bars 100 µm, 50 µm. **D**. Sectional view of stolonal triad on main stem, looking distally (ZPAL G.30/11). Scale bar 50 µm. **E**. Stolonal triad on main stem, looking proximally; diaphragm at base of occluded autotheca (arrowed) (ZPAL G.30/12). Scale bar 50 µm. **F**. Base of diaphragm on main stem, looking distally, and showing two pores (ZPAL G.30/13). Scale bar 10 µm. **G**. Portion of stem with monopodial branch to right. *a*, occluded first thecal base on branch, with short stolotheca. *b*, borings on main stem (ZPAL G.30/14). Scale bar 500 µm.

Stipes

Stipes are understood here to be an extension of a short and unbranched stem. After isolation from the matrix they preserve primary flexibility. During life, they were strong enough to support an enigmatic epibiont, *Clistrocystis graptolithophilius*, later interpreted as probable cephalopod eggs, laid down on *Mastigograptus* colonies (Kozłowski 1959, 1965).

Stipes are in fact chains of interconnected stolothecae, covered by thick cortex and provided with alternately placed (right and left) broken bases of thecal groups (producing characteristic swellings), spaced at regular intervals of about 1 µm. These free portions of thecae were made of fragile fusellar fabric, with none or scarce cortical deposits. They were preserved in specimens described by Andres (1961, 1977), while in our material they are completely detached leaving only characteristic scars, or the initial portion of the thecae (thecal bases, see above p. 448). Also internal stolons may be seen through such scars. A stipe branch (Figs. 3D, 4G) also tends to occur at such broken bases of thecal groups, and will leave the main stipe as a monopodial branch, in the same direction as the thecal tube which it replaces (Andres 1977: fig. 15). In our material, we can only see the broken bases of the thecal tubes where their walls are very thin (Fig. 2G, H), and the initial portions of the tubes where they are thicker (Figs. 3A, G, 8E).

The stipe in dendroids is a compact structure, made of a stolonal chain (or chains) and adnate auto- and bithecae, grouped on one side or surrounding the stolothecae. The construction of the stipe in *Mastigograptus* is distinctly non-dendroid: while the stipe proper is produced by a chain of heavily corticalized stolothecae, the remaining thecae project freely. In dendroids, auto- and bithecae are usually adnate throughout the length to stolonal chain, or at least adnate proximally and isolate distally to a varying extent (as in *Acanthograptus*). Therefore, the dendroid stipe is essentially a bunch of adnate thecae. Freely projecting, conical and relatively large, completely isolated thecae in *Mastigograptus* are similar to rhabdopleurids or to so-called dithecoids (see p. 457) and represent a primitive condition as compared with dendroid and tuboid (tubidendroid) colonies.

Proximal stolothecal segments of the stipe are tubular, almost parallel-sided (50–80 µm in diameter), with a very slight swelling towards the upper two-thirds of the segment (Figs. 1G, 3D). They have an internal lumen of about 40? µm in diameter, and a wall thickness of 40 µm. The thecal bases (points of attachment, "Ansatzstellen" of Andres 1977) are, like the occluded sicular aperture, situated on inclined shelves in a slight swelling of the stipe (Figs. 2G, H, 3C); they have thin ragged rims and a diameter of about 40 µm. Two specimens (Fig. 3B, C), although damaged, appear to show that the first thecal base was occluded. This could have been either because the thecal tube(s) did not develop beyond this point, or that they were removed before the hole was sealed.

Distal stolothecal segments of stipes become conspicuously greater in diameter at two-thirds the length of a segment, to become vase or amphora-shaped (Figs. 3G, 8E), narrowing markedly at the nodes. Lumen diameter at just above the swellings (Fig. 3A) is about 80 µm, with a wall thickness of about 50 µm. Stolothecal segments broken at their distal end just below the neck of the amphora (Fig. 3H), show a large internal lumen (280 × 130 µm in one specimen; 170 µm in a needle preparation from another specimen) and thin walls (30 µm). Among the isolated material are some partially flattened specimens (Fig. 3G). The fact that these have become flattened suggests that they were young stipes that had not yet acquired the substantial thickening of the wall (to about 100 µm) commonly seen in more mature parts of the colonies. From this it may be deduced that the amphorate segments were built with this shape, rather than acquiring it by thickening of the cortex. The same is indicated by specimens illustrated by Andres (1977: fig. 13) showing a thin-walled theca (stolotheca?), devoid of any cortex but exhibiting an amphorate shape (inflated middle portion with narrowing neck).

The fusellum is built of distinct fuselli (Figs. 4A, 7E), about 10–20 µm in height and 3–5 µm in thickness. Owing to the thickness of the cortex, it was not possible to see zig-zag or other sutures between fuselli. Each fusellus has a core of fusellar fabric, bounded by a sheet fabric (Fig. 4A).

As in the basal disc, the cortex is formed of units comprising parallel fibrils forming a cortical fabric, bounded by sheet fabric with scattered vesicles (seen in the TEM sections of Urbanek and Towe 1974: pls. 19–21). Each unit (Fig. 4A) is about 2 µm thick, with closely packed parallel fibrils, about 300 nm in diameter, making up the bulk of the unit; within each unit the fibrils are packed about 8–10 deep. A sheet fabric bounds each unit. We were not able to distinguish any edges of cortical units: either parallel edges defining bandages, or more irregular boundaries. This is probably because the edges of units are extremely thin, with no cortical fabric beneath, as seen in the TEM sections of Urbanek and Towe (1974: pls. 2, 21–22).

A curious surface pattern of low ridges is sometimes seen on the surface of the cortex (Fig. 4B, C). On one side of the stipe the ridges sweep forwards, towards the distal end of the stipe; on the other they sweep backwards (Fig. 4C). On the sides of the stipe which contain the thecal bases, there is an interlaced pattern (Fig. 4B). The ridges probably represent the direction of the parallel cortical fibrils in the units beneath, but even so we have been unable to determine the shape of the cortical units.

The thecal bases diverge at an angle of about 50° from the main stipe, but quickly bend to become almost parallel to it (Fig. 4G). They have an ovoid cross-section, with the short axis of the cone directed towards the main stipe. At about 300? µm from the main stipe (Figs. 3I, 8E, M) they expand into a triangular "head". At the corners of the head are circular holes, fringed with ragged tissue: these may be the bases of the thin flaring thecal tubes illustrated by Andres. Between them is an oval area, outlined by a rounded ridge but floored by cortex rather than an opening into the interior. The shape of the whole head is alarmingly reminiscent of that of the fictional extra-terrestrial "E.T.", from the film of the same name!

According to Andres (1977: 67), branching is either dichotomous or irregularly monopodial. Specimens studied in some detail by us show monopodial budding. At places where a stipe branches (Figs. 3D, 4G), a monopodial branch replaces the normal thecal base. An ?occluded thecal base occurs a short distance up the branch (Fig. 4G, a), followed by the first segment of the branch of normal length. A similar thecal base can be seen in a specimen figured by Andres (1977: fig. 15).

Internal structure

Andres (1961, 1977), using the light microscope and bleached and unbleached specimens, has illustrated thecal groupings, and shown a diagram of the proximal part of a thecal triad (1977: fig. 20) situated "a little below the region where the thecae detach from the stem (stipe)". The narrow canal of the "central theca" is depicted in the front of the diagram. In the light of studies on budding pattern in dendroids (especially Kozłowski 1938, 1949; Bulman 1944, 1973) the proximal part of the triad figured by Andres corresponds to the internal portions of thecae following a node and trifurcation of the stolon seen inside a parental stolotheca. The narrow canal of the "central theca", ending with a shallow cup, certainly corresponds to the stolon and internal part of an autotheca, while the two laterally situated wider tubes correspond to the internal parts of the lateral thecae of the triad (either a stolo- or a bitheca). It seems from our data (Fig. 5, base of triad) as well as from Andres' (1977: figs. 17–19) observations on transparent specimens that lateral thecae lack their own stolons. Above the diaphragm (on Andres' figures depicted as a thicker line) lateral thecae represent internal portions of thecae inside the parental stolotheca.

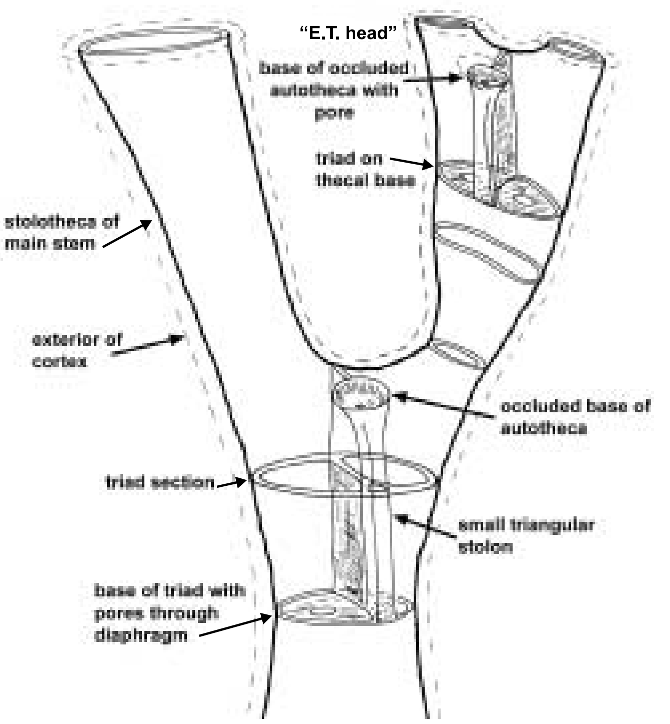

Fig. 5. *Mastigograptus* aff. *tenuiramosus*. Diagram showing internal structure of stem with thecal triads and thecal base. Not to scale.

The transverse septum, dividing the cavity of the parental stolotheca and depicted by Andres (1977: fig. 20) as a single wall, was in fact produced by the close contact of two internal portions of thecae, as demonstrated in our SEM micrographs (Fig. 4D). Andres (1961, 1977) was unable to establish safely any size differences between the lateral thecae in his *Mastigograptus* material, and concluded that, if present, thecal dimorphism must be smaller than among the Dendroidea and Crustoidea. Our observation on thecal bases likewise do not reveal any differences between lateral thecae. Therefore, the use of dendroid thecal terminology is tentative until more data become available, although there is no doubt that the budding pattern in *Mastigograptus* rigidly follows Wiman's rule. Andres recognised these thecal triads only on the main stem: however, our observations show that in each thecal base there is a second thecal triad (see Fig. 5).

Stolothecal segments

Individual stolothecal segments of stipe, except those from just below the thecal bases, have relatively wide lumens (Figs. 3F, H, 5) in which there appears to be no internal stolon (which should, if comparable to that in normal Dendroidea, be a narrow and thin-walled tube lying within the lumen, and not necessarily centred on the axis of the segment). Andres was unable to find evidence of the stolon in his material (e.g. 1977: fig. 18). However, Urbanek and Towe (1974: pl. 21, pl. 22: 1, see also diagram Fig. 2) figured a cross-section of a segment of stipe, which shows a wall formed of an outer cortex (at least 8 μm thick), a relatively thin (0.5–3.0 μm) fusellar unit, and an inner lining of dense crassal fabric 0.6–2.8 μm thick. These layers can be recognised in our broken segment walls: a thick cortex (Fig. 3F), composed, like the laminae of the holdfast, of units of parallel fibrils separated by lamellae of sheet fabric; a thin fusellar wall (Fig. 4A); and an inner lining of dense and uniform material (Fig. 7D, E). The inner lining of crassal fabric we tentatively interpret as being the wall of stolothecal stolon – which then occupies the whole of the space within the stolothecal segment, and the actual lumen is the space within the stolon. Each segment of the stipe is therefore a stolotheca, in the conventional terminology as applied to dendroid graptolites, although its stolon differs from that of standard dendroids. It resembles, however, the stolon in *Rhabdopleurites*, a fossil rhabdopleurid revealing inflated and narrow portions in an irregular succession (Kozłowski 1970: pl. 2: 4, 5). If our comparison is correct, in *Mastigograptus* even more inflated portions are regularly spaced. More light may be shed on the nature of the stolon in *Mastigograptus* by a study of closely related *Micrograptus*.

The crassal lining of the stolothecal segments has been exposed in a number of broken sections (Fig. 7D–F, arrowed). It is extremely thin (Fig. 7D, E), but clearly comprises of more than one layer, as one sheet of fabric ends in an irregular margin. The diaphragm of a stolonal triad is shown in Fig. 7D and F, the extremely thin crassal lining becomes thicker towards the diaphragm, which is about 3–4 μm thick. Hence, there is a continuity between the crassal lining of the stolotheca proper and crassal sheath of the stolonal triad. This one of the reasons why we are inclined to ascribe the role of stolonal sheath to the inner lining of stolothecae in *Mastigograptus*. The other reason is a remarkable similarity of crassal fabric in the inner lining of the latter to stolonal material recognized with TEM in some dendroid graptolites (Urbanek and Towe 1974: pl. 4: 1–2). Otherwise the inner lining is a widely spread feature among graptolites (see also Andres 1980; Mierzejewski 1984). In each case it is organized in a somewhat different way and hardly may be homologized. We share the opinion of Andres (1980: 145) that the inner lining in *Mastigograptus* is a special structure of this genus, which in this form has not been found in other graptolites. Nevertheless, our interpretation of the structure in question as a *sui generis* stolonal sheath is tentative. The other possible interpretation is that stolothecal segments of stolon in *Mastigograptus* were of normal type but were devoid of skeletal sheath and therefore are not preserved. If sclerotized, stolons belong to most resistant skeletal part of the rhabdosome and should be preserved.

The budding pattern of *Mastigograptus*, as revealed by the material studied herein, is essentially comparable with the triad plan, recognized in dendroids and crustoids (Kozłowski 1949, 1962) . This basic pattern is, however, modified in some cases, mainly by the production of abortive (occluded) thecae.

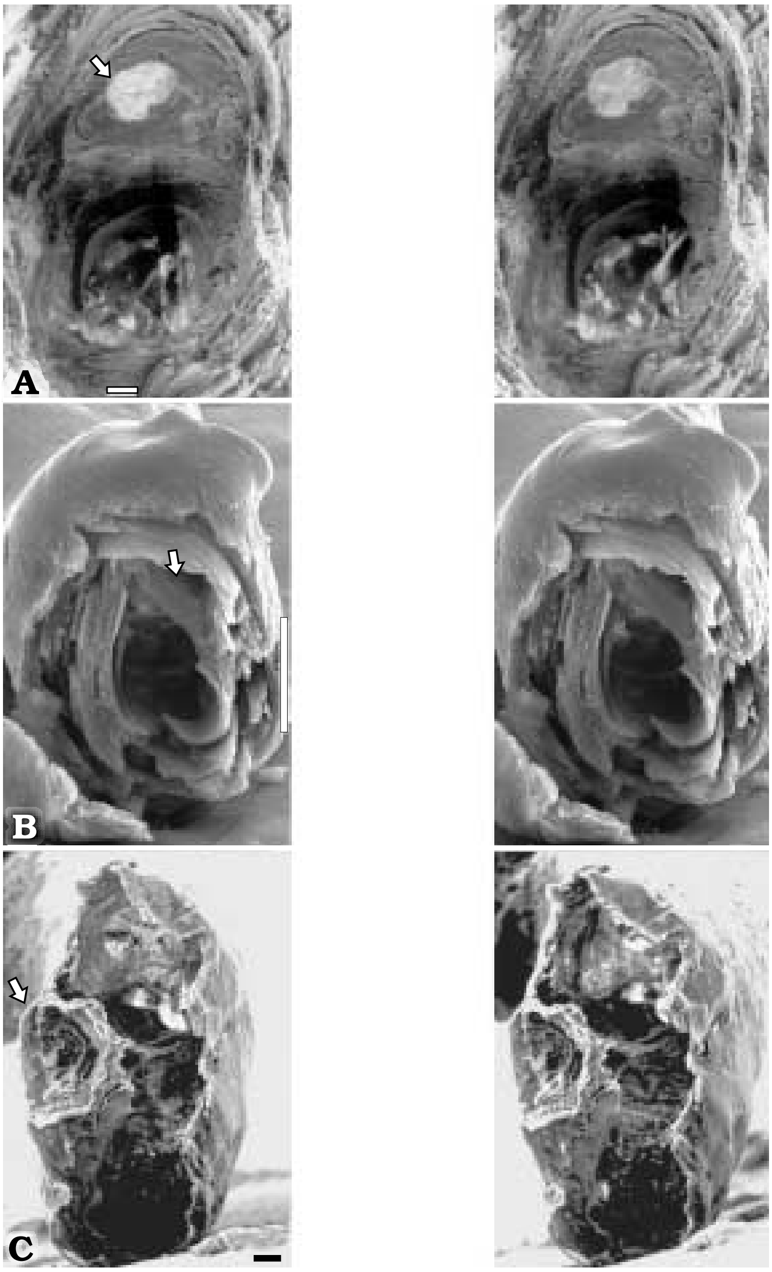

Fig. 6. *Mastigograptus* aff. *tenuiramosus*. **A**. Stereopair of triad of stolotheca; diaphragm of stolon leading to thecal base arrowed (ZPAL G. 30/15). Scale bar 10 μm. **B**. Stolonal triad on main stem, close to thecal base. Lower canal leads to the next section of the stem; upper canal (arrowed) leads to the thecal base, a needle preparation from ZPAL G. 30/10. Scale bar 50 μm. **C**. Stereopair of stolonal triad in thecal base, including occluded autotheca (arrowed), looking proximally (ZPAL G. 30/15). Scale bar 10 μm.

Thecal triads (see Fig. 5) can be identified in a number of segments, by looking distally along a segment, or where it is broken just below a thecal base. The basal portion appears to form a transverse partition or diaphragm (Fig. 4F), pierced by pores (two only can be seen in this specimen). In the next stage, a typical dendroid triad is formed of dense crassal fabric (Figs. 4D, E, 6A, B diaphragm arrowed, 7C). The stipe has here become oval shaped, as it approaches the thecal base, and this space is occupied by two large stolonal tubes of lateral thecae, which abut against each other centrally, but remain discrete, and a much smaller and triangular-shaped stolon of a central theca is “compressed” into a space left between the two larger stolons and the surrounding wall of the stipe (Fig. 7A, B). The long axis of the oval lies in the plane containing the stipe and the thecal base, and it would appear that one of the large stolonal tubes should continue into the next stolonal segment of the stipe (Fig. 5, stolotheca of main stem), and the other into the base of a free theca. In one specimen (Fig. 6A) the triad is broken obliquely, so that the stereopair shows different levels in the structure, with a restricted pore in the diaphragm of the stolon leading to the thecal base.

By comparison with the dendroids, the small triangular tube should lead to the base of an autotheca. Here it ends in a small diaphragm, pierced by a central pore (Figs. 4E, 5). However, each thecal base has only a single tube within it – that leading from one of the main tubes of the triad (Figs. 3A, 8A, F, G). In some lightly corticised specimens (Fig. 8B, C), there appear to be two openings, one corresponding to the main tube

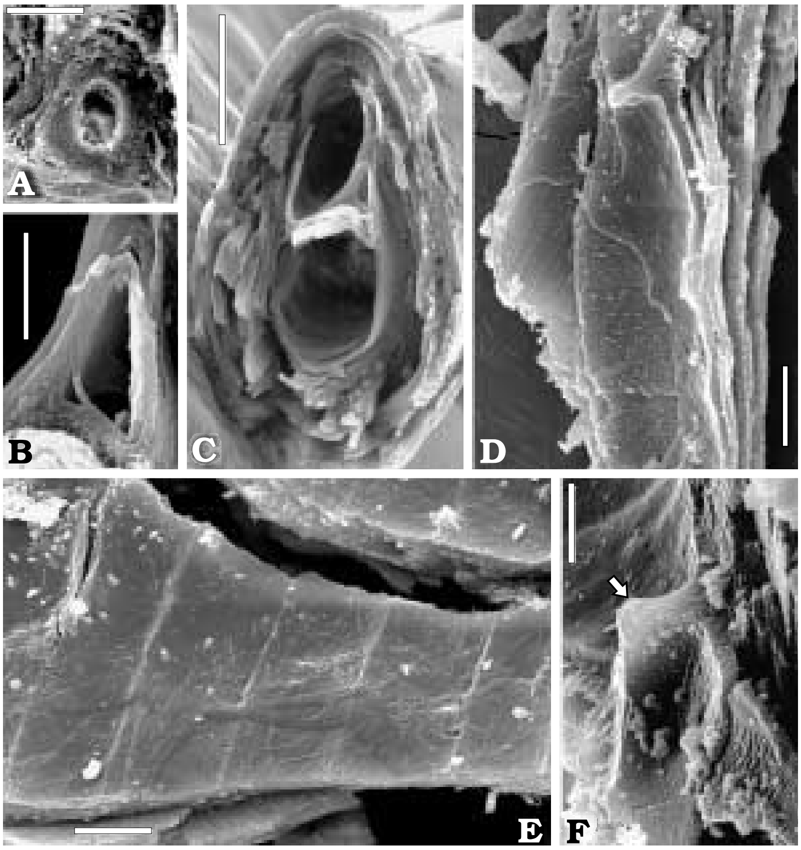

Fig. 7. *Mastigograptus* aff. *tenuiramosus*. **A**. Small autothecal stolon in triad of stolotheca of Fig. 6A. Scale bar 10 µm. **B**, **C**. Autothecal stolon in triad on main stem (ZPAL G.30/16). Scale bars: **B**, 10 µm; **C**, 50 µm. **D**, **F**. Crassal lining of portion of stolotheca, with fractured diaphragm (arrowed), a needle preparation from ZPAL G.30/10. Scale bars 10 µm. **E**. Crassal lining of portion of stolotheca, a needle preparation from ZPAL G.30/12. Scale bar 20 µm.

of the branch, and the other to a smaller depression. This latter appears to be underlain by a small space, formed at the distal end of the small triangular tube (Fig. 8D). In more heavily corticised portions of the stipe there is no external sign of this structure (Fig. 8E). Therefore the autotheca (of which the previous stolotheca is in fact the proximal portion) cannot have persisted as an open tube as growth of the colony continued. The aperture, if it was initially present, has become occluded.

Thecal bases

In specimens where the stolothecal branch tube is broken close to its origin from the stipe, it is circular in cross-section (Figs. 2G, H, 3A) and, like the main segments, appears not to have any stolonal tubes within it. A little further away, the cross-section is slightly dumb-bell shaped (Fig. 8F). It also has a lining of crassal fabric (Figs. 3F, 5, 8G) and hence can also be interpreted as having its lumen filled completely by a stolon.

Further broken specimens show that within the "E.T. head" of the thecal base, there is a second stolonal triad, with the same morphology as that in the main stipe (Fig. 5, triad on thecal base). The tube becomes ovoid, with the short axis of the oval parallel to the plane containing the stipe and the thecal tube, and the small triangular stolon at the side facing the main stipe (Fig. 8E, H, K arrowed)). Proximal to this there is a transverse diaphragm pierced by pores (Fig. 8J). Distally, as the head expands, the triad widens; the small stolon leads to a small concave region (Fig. 6C), and the two larger stolons to the holes forming the "eyes" of the "E.T. head".

In all the material available, the two holes have ragged and rather thin edges (Figs. 3F, 8M), in contrast to the thicker walls of the head and thecal base, and are clearly not the actual apertures of any theca. Presumably thin-walled thecae, as illustrated by Andres (1977: fig. 13), extended from them, but have been torn off in our material. Between these two lateral holes, there is a distinct transversely oval ridge with a rounded crest, surrounding a slightly depressed area (Fig. 8I, M). It corresponds in position, size and shape to the concave region beneath, and hence should form a roof to the latter. As with the sicula and proximal thecal bases, this is probably an occluded aperture, in this case of an aborted autotheca, on the assumption that the narrow triangular stolon of the triad is homologous with that in a dendroid, as described by Kozłowski (1949) and Bulman (1944, 1973).

Each thecal base then contains a stolonal triad, but only two apertures. Similarly, each triad on the main stipe leads to two tubes: one the stolotheca forming the next section of the stipe, and the other the stolotheca forming the thecal base leading to the "head", with the next triad. However, here also the narrow stolonal tube cannot lead to an aperture, but must have been occluded, probably at the level of separation of the thecal base from the stipe.

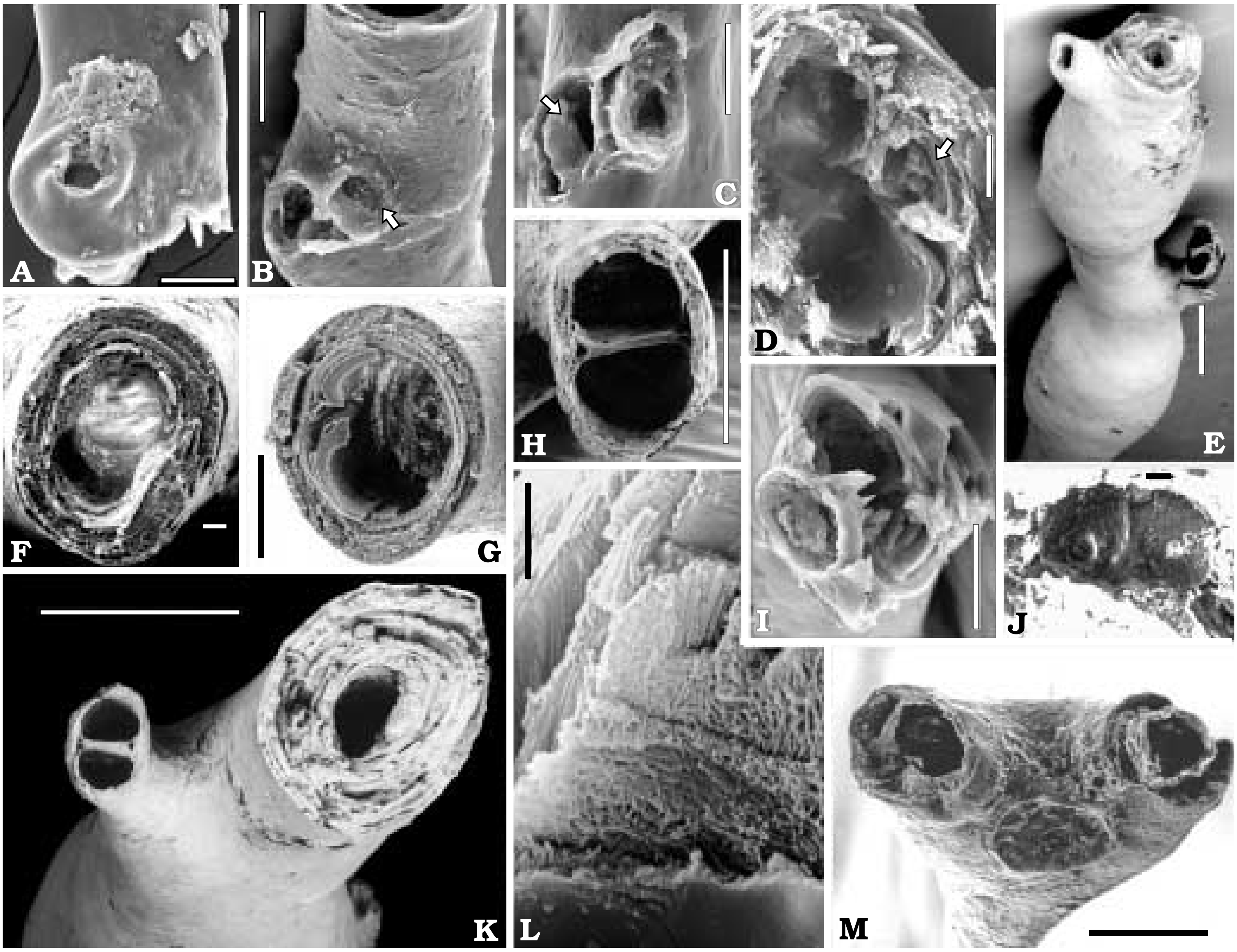

Fig. 8. *Mastigograptus* aff. *tenuiramosus*. **A**. Thecal base of Fig. 6B. Scale bar 50 µm. **B**, **C**. Fractured thecal bases, and occluded autotheca (arrowed) (ZPAL G.30/17). Scale bars: **B**, 100 µm, **C**, 50 µm. **D**. Thecal base on main stem, with occluded autotheca (arrowed), a needle preparation from ZPAL G.30/18. Scale bar 20 µm. **E**. Stem, looking obliquely proximally, with two thecal bases (ZPAL G.30/15). Scale bar 200 µm. **F**, **G**, **H**. Successively more distal cross-sections of thecal bases. Scale bars 10 µm, 50 µm, 100 µm. **I**. Thecal base with occluded autotheca (ZPAL G.30/17). Scale bar 50 µm. **J**. Diaphragm of stolonal triad in thecal base, looking proximally (ZPAL G.30/15). Scale bar 10 µm. **K**. Stolotheca looking proximally with adjacent thecal base displaying a stolothecal triad, see H (ZPAL G.30/11). Scale bar 200 µm. **L**. Crassal, fusellar and cortical tissues in thecal base (ZPAL G.30/17). Scale bar 5 µm. **M**. "E.T. head" of thecal base, with central occluded autotheca (ZPAL G.30/4). Scale bar 50 µm.

At a stipe branching there should be a similar triad formed in the main stipe, and the "head" would appear to be modified to allow one of the large stolonal tubes to extend as a thin-walled thecal cup, and the other as the first fully developed segment of the branch.

If we attempt to homologise the triads in *Mastigograptus* with this scheme, it appears that each triad in the main stipe must have two stolothecae leading from it: one prolonging the stipe, and one leading into the thecal base. In turn it would seem that the same pattern is present in the head of the thecal base: again two stolothecae are produced, leading to the two thecal cups. All apertures formed from the thin triangular central stolons are occluded.

Systematic position

The systematic position of *Mastigograptus* has long remained an open question. Without any proper knowledge of the structural details, this genus was provisionally classed as a hydroid coelenterate (Ruedemann 1908, 1947; Chapman 1919, 1936). Bulman (1938) placed it among genera of uncertain systematic affinity, possibly related to hydroids, but later (Bulman 1955) assigned it to his newly erected dendroid family, the Chaunograptidae. However, in the 2nd edition of the Treatise (Bulman 1970) we find *Mastigograptus* again among genera whose order and family are uncertain. The Chaunograptidae were later removed provisionally to the hydroids by Rickards (1993), although this cannot include *Mastigograptus*, assigned by Bulman (1955) with the type-genus and two more dubious genera to this family. As a matter of fact, Andres (1961) provided convincing evidence that *Mastigograptus* is a graptolite. After studying his isolated specimens of the genus in question Kozłowski (1962: 31) arrived at the opinion that it differs so distinctly from the Dendroidea and Crustoidea as to represent an order of its own. This suggestion of Kozłowski passed unnoticed by later students. Obut (1964) assigned *Mastigograptus* to the order Dithecoidea, a new group established by him to embrace primitive graptolites preceding dendroids and for some time co-occurring with them, and placed it in the family Chaunograptidae. He paid no attention to the earlier paper by Kozłowski (1962), who provided evidence for great differences in stolon system and colony pattern separating *Chaunograptus* and *Mastigograptus*. The idea of a dithecoid affinity of the latter proved to be persistent: Sdzuy (1977) treated it as a representative of the Dithecoidea, while Andres (1977), without drawing taxonomic conclusions, emphasized its resemblance to dithecoids (such as lack of dimorphism in freely projecting thecae). More recently this point of view was elaborated by Chapman, Durman and Rickards (1996). In their considerations based largely on the still unpublished doctoral thesis of Durman, *Mastigograptus* is treated as a representative of Dithecoidea occupying an intermediate position towards Dendroidea. Moreover, they argue that dendroids developed directly from mastigograptids *via* transformation of free thecae into adnate ones, which are characteristic of the dendroid condition.

In an attempt at evaluation of the entirety of data available we are going to argue for the point of view first advanced by Kozłowski (1962), namely (1) that *Mastigograptus* (and the related genus *Micrograptus*) represent a distinct family (the Mastigograptidae fam. nov., for diagnosis see below), moreover (2) that this family cannot be placed within either the Dendroidea or the Dithecoidea, but belongs to a separate, new order of Graptolithina (Mastigograptida ord. nov., for diagnosis see below). The structure of mastigograptids is a mosaic of dendroid, pterobranch and unique characters. Among the essentially dendroid elements are: cylindrical sicula provided with basal disc, budding following the Wiman Rule (which however *per se* cannot define their assignement to Dendroidea), and general dendroid shape of the colony. This latter feature, however, seems misleading, because of the non-dendroid construction of stipes (see above). Non-dimorphic, thin walled and freely projecting thecae, as well as their complete fuselli, lacking the zig-zag suture—all resemble the pterobranch condition. Stolothecae display a morphological gradient expressed in size increase and change of shape—an unexpected feature for a sessile graptolite with *Mastigograptus* morphology, known so far only in anisograptids and graptoloids. Moreover, the structure of the stolothecal stolon, namely its presumed strong inflation, as described above, is a peculiar feature, with so far some analogy only among the fossil Rhabdopleurida. Although the *Mastigograptus* clade has attained the graptolite structural grade, it preserves some primitive features, suggesting a close relationship with rhabdopleurid ancestors (e.g., the essentially pterobranch appearance of the free portions of its thecae, as compared with truly graptolitic character of stolothecae—an instance of mosaic evolution).

Therefore, *Mastigograptus* and its allies should not be assigned to the order Dendroidea, and be placed in a distinct position as an independent order within Graptolithina. In recent classification schemes suggested for the order Dendroidea Nicholson, 1872 (see Rickards 1993) there is no place for genera which represent *Mastigograptus* morphology. On the other hand Chapman, Durman, and Rickards (1996: 195) consider the genus in question as morphologically intermediate between dithecoids and dendroids, suggesting that it may be as well the evolutionary link between the Dithecoidea and Dendroidea. However, their concept of transformation of a mastigograptid into a dendrograptid *via* a simple change in arrangements of autothecae from free into adnate needs certainly more evidence that this provided by their fig. 6. A rather close relation of mastigograptids to some stem dendroids is, however, probable.

Well established budding pattern in triads combined in *Mastigograptus* with only incipient (or no) dimorphism may indicate the order of appearance of these apomorphic features in the phylogeny. If we consider after Kozłowski (1949) that differences between auto- and bithecae reflect sexual differences between fully developed female (later hermaphroditic) zooids and partly reduced male zooids respectively, the character states observed in *Mastigograptus* speak in favour of their almost equal development, resembling the pterobranch conditions (small size differences, however, were noted for the male and female zooidal tubes in *Rhabdopleura*). Also the fusellar tissue studied in detail by Andres (1977) bears many pterobranch (rhabdopleurid) features, such as the presence of fuselli producing complete rings and their oblique sutures showing an essentially irregular arrangement (with an observed tendency toward their more regular placement, resembling the zig-zag suture of regular graptolites). The last two features are frequently quoted as arguments in favour of dithecoid affinities of mastigograptids. However, the concept of Dithecoidea remains vague and poorly defined, largely because their remains are badly preserved and insufficiently studied. The group seems highly heterogenous and therefore artificial (Mierzejewski 1986). The only common features diagnostic for the group are: presence of free projecting thecae and absence of their dimorphism. Both are plesiomorphic in nature, retained from presumable rhabdopleurid ancestors. That sessile orders of graptolites were preceded by some transient group, displaying a number of rhabdopleurid characters seems to be a safe conclusion. However, whether this transient group corresponds to Dithecoidea as defined by Obut (1964) is another question. Therefore we prefer to follow Kozłowski's suggestion and propose a new order of Graptolithina to include *Mastigograptus*:

Order Mastigograptida nov.

Diagnosis.—Cylindrical sicula, budding in triads, dendroid habitus but stipes produced by chain of corticalized stolothecae with thin-walled free thecae, displaying random arrangements of oblique sutures, and not revealing a distinct dimorphism.

Stratigraphic distribution.—Cambrian–Silurian.

Family Mastigograptidae nov.

Diagnosis.—As for the order.

Genera included.—*Mastigograptus* Ruedemann, 1908 (Cambrian–Silurian); *Micrograptus* Eisenack, 1974 (Ordovician).

Acknowledgements

We thank Dr. Cyprian Kulicki (Warsaw) for his assistance when using the SEM. Thanks are also due to Mrs. Aleksandra Hołda for her help in improving our drawing for Fig. 5. The preparation of this paper was facilitated by A. Urbanek's visit (1996) to Aberystwyth within the framework of exchange between The Royal Society of London and the Polish Academy of Sciences, as well as by D.E. Bates' visit in 2001 to Warsaw, as part of a NERC (UK) grant. Our paper benefited much from remarks and improvements suggested by Dr. Peter R. Crowther (Belfast) as well as by an anonymous reviewer.

References

Andres, D.1961. Die Struktur von Mastigograptiden aus einem ordovizischen Geschiebe Berlins. *Neues Jahrbuch für Geologie und Paläontologie* 12: 636–647.

Andres, D. 1976. *Graptolithen aus ordovizischen Geschieben und die frühe Stammesgeschichte der Graptolithen.* Inaugural-Dissertation zur Erlangung der Doktorwürde (Freie Universität Berlin). 75 pp. Berlin.

Andres, D. 1977. Graptolithen aus ordovizischen Geschieben und die frühe Stammesgeschichte der Graptolithen. *Paläontologische Zeitschrift* 51: 52–93.

Andres, D. 1980. Feinstrukturen und Verwandschaftbeziehungen der Graptolithen. *Paläontologische Zeitschrift* 54: 129–170.

Bates, D. 1997. The ultrastructure of a Silurian dendroid from Gotland (Sweden). *Geobios* 20: 27–37.

Bulman, O.M.B. 1938. Graptolithina. *In*: O.H. Schindewolf (ed.), *Handbuch der Paläozoologie 2D*, D1– D92. Berlin.

Bulman, O.M.B. 1944. *Caradoc (Balclatchie) Graptolites from Limestones in Laggan Burn, Ayrshire*, I. 78 pp. Palaeontographical Society Monographs, London.

Bulman, O.M.B. 1955 Graptolithina (with sections on Enteropneusta and Pterobranchia) (1st edition). *In*: R.V. Moore (ed.), *Treatise on Invertebrate Paleontology* V, 1–101, New York.

Bulman, O.M. B. 1970. Graptolithina (with sections on Enteropneusta and Pterobranchia) (2nd edition) *In*: R.V. Moore (ed.), *Treatise on Invertebrate Paleontology* V, 1–101. New York.

Bulman, O.M. B. 1973. Graptolite periderm structure and budding patterns. A Resumé *In*: G.P. Larwood (ed.), *Living and Fossil Bryozoa*, 11–20.

Chapman, F. 1919. On some hydroid remains of Lower Palaeozoic age from Monegetta near Lancefield. *Proceedings of the Royal Society of Victoria* 31 (N.S.): 388–393.

Chapman, F. and Thomas, D.E. 1936. The Cambrian Hydroida of the Heathcote and Monegeeta Districts. *Proceedings of the Royal Society of Victoria* 48, Part II (N.S.): 193–212.

Chapman, A.J., Durman, P.N., and Rickards R.B. 1996. A provisional classification of the graptolite Order Dendroidea. *Paläontologische Zeitschrift* 70: 189–202.

Eisenack, A. 1934. Neue Mikrofossilien des baltischen Silurs, III. *Paläontologische Zeitschrift* 16: 52–76 .

Eisenack, A. 1974. Einige neue Graptolithen aus dem Ordovizium des Baltikum, ferner über *Epigraptus* und andere Idiotubidae. *Neues Jahrbuch für Geologie und Paläontologie* 11: 664–674.

Kozłowski, R. 1938. Informations preliminaires sur les graptolithes du Tremadoc de la Pologne et leur portée théorique. *Annales Musei Zoologici Polonici* 13: 183–196.

Kozłowski, R. 1949. Les graptolithes et quelques nouveaux groupes d'animaux du Tremadoc de la Pologne. *Palaeontologia Polonica* 3: 1–235.

Kozłowski, R. 1959. Un fossile enigmatique. *Acta Palaeontologica Polonica* 4: 273–277.

Kozłowski, R. 1962. Crustoidea – nouveau groupe de graptolithes. *Acta Palaentologica Polonica* 7: 1–52.

Kozłowski, R. 1965. Oeufs fossiles de cephalopodes? *Acta Palaeontologica Polonica* 10: 3–9.

Kozłowski, R. 1966. On the structure and relationships of graptolites. *Journal of Paleontology* 40: 489–501.

Kozłowski, R. 1970. Nouvelles observations sur les rhabdopleuridés (ptérobranches) ordoviciens. *Acta Palaeontologica Polonica* 15: 3–13.

Mierzejewski, P. 1984. *Pterobranchites* Kozłowski, 1967 – an aberrant graptolite? *Acta Palaeontologica Polonica* 29: 83–89.

Mierzejewski, P. 1986. Ultrastructure, taxonomy and affinities of some Ordovician and Silurian organic microfossils. *Palaentologia Polonica* 47: 129–220.

Obut, A.M. 1964. Subphylum Graptolithina [in Russian]. *In*: Û.A. Orlov, (ed.), *Osnovy paleontologii, 10*, 284–357. Nedra, Moskva.

Rickards, R.B. 1993. Graptolithina. *In*: M.J. Benton (ed.), *The Fossil Record*, 2, 537–542. Chapman & Hall, London.

Ruedemann, R. 1908. Graptolites of New York. Pt. II Graptolites of the Higher Beds. *New York State Museum Memoirs* 7: 4–583.

Ruedemann, R. 1947. The graptolites of North America. *Memoirs Geological Society of America* 19: 1–652.

Sdzuy, K. 1974. Mittelkambrische Graptolithen aus NW-Spanien. *Paläontologische Zeitschrift* 48: 110–139.

Skevington, D. 1963. Graptolites from the Ontikan Limestones of Öland, Sweden, I: Tuboidea, Camaroidea, and Stolonoidea. *Publications of Paleontological Institution, University of Uppsala* 46: 1–62.

Urbanek, A. 1959. Studies on graptolites II. On the development and structure of graptolite genus *Gymnograptus* Bulman. *Acta Palaeontologica Polonica* 4: 179–338.

Urbanek, A. and Towe, K.M. 1974. Ultrastructural studies on graptolites, I: The periderm and its derivatives in Dendroidea and in *Mastigograptus*. *Smithsonian Contributions to Paleobiology* 20: 1–48.